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(2019)

DOI (TUprints): <https://doi.org/10.25534/tuprints-00013333>

Lizenz:



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Publikationstyp: Article

Fachbereich: 03 Department of Human Sciences

Zentrale Einrichtungen

Quelle des Originals: <https://tuprints.ulb.tu-darmstadt.de/13333>

The visual control of interceptive steering: How do people steer a car to intercept a moving target?

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The visually guided interception of a moving target is a fundamental visuomotor task that humans can do with ease. But how humans carry out this task is still unclear despite numerous empirical investigations. Measurements of angular variables during human interception have suggested three possible strategies: the pursuit strategy, the constant bearing angle strategy, and the constant target-heading strategy. Here, we review previous experimental paradigms and show that some of them do not allow one to distinguish among the three strategies. Based on this analysis, we devised a virtual driving task that allows investigating which of the three strategies best describes human interception. Crucially, we measured participants' steering, head, and gaze directions over time for three different target velocities. Subjects initially aligned head and gaze in the direction of the car's heading. When the target appeared, subjects centered their gaze on the target, pointed their head slightly off the heading direction toward the target, and maintained an approximately constant target-heading angle, whose magnitude varied across participants, while the target's bearing angle continuously changed. With a second condition, in which the target was partially occluded, we investigated several alternative hypotheses about participants' visual strategies. Overall, the results suggest that interceptive steering is best described by the constant target-heading strategy and that gaze and head are coordinated to continuously acquire visual information to achieve successful interception.

Introduction

Successful interaction with moving objects in complex and dynamic environments is vital to humans' survival. Locomotor interception of a moving target is challenging because we need to coordinate our movements with the target's movements. Whether traveling on foot (Rushton, Harris, Lloyd, & Wann, 1998) or using a vehicle (Wilkie & Wann, 2002), whether chasing a flying ball in sports (Chapman, 1968) or using the so-called precision immobilization technique in car chases (Zhou, Lu, & Peng, 2008), the challenge is analogous to the one faced by a predator chasing its prey. Surprisingly, a comprehensive algorithmic description of how humans accomplish these tasks is still not available despite considerable research efforts. Here, we make progress toward understanding the strategies employed by humans by empirically investigating how locomotor interception is visually guided when participants steer a car to intercept a moving target in a virtual environment. Specifically, we examine how peoples' gaze and head are coordinated with their steering to guide such interceptions. The present empirical study quantifies the regularities in human interception behavior, which is an important step toward finding a computational account of the interception of moving targets.

Citation: Zhao, H., Straub, D., & Rothkopf, C. A. (2019). The visual control of interceptive steering: How do people steer a car to intercept a moving target? *Journal of Vision*, 19(14):11, 1–20, <https://doi.org/10.1167/19.14.11>.

<https://doi.org/10.1167/19.14.11>

Received May 30, 2019; published December 12, 2019

ISSN 1534-7362 Copyright 2019 The Authors



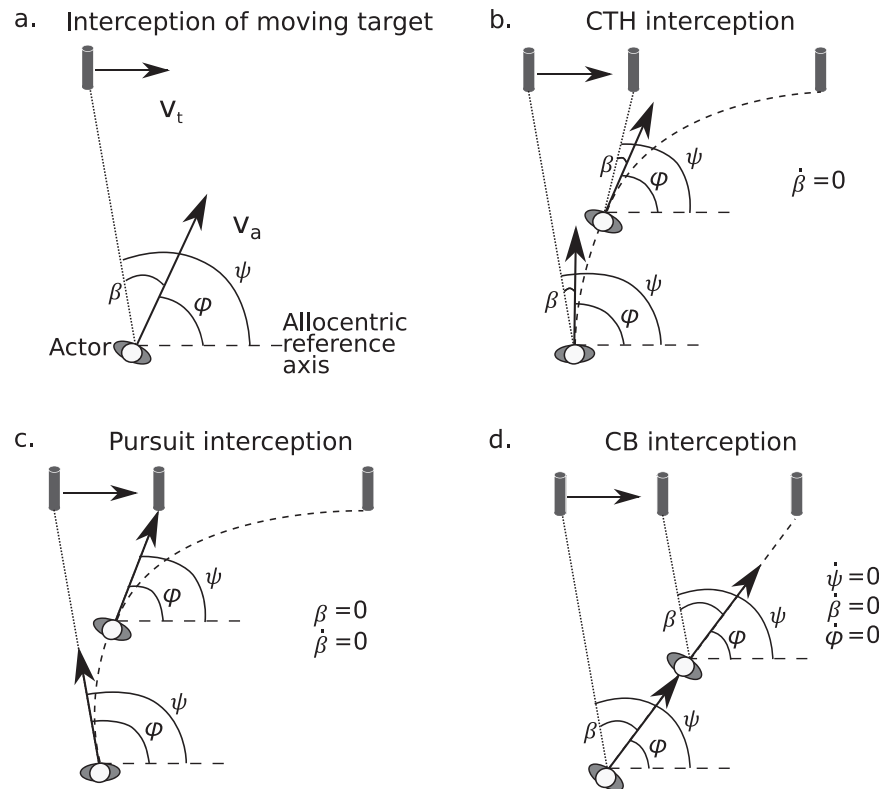


Figure 1. Different interception strategies and their associated angular quantities. (a) Definition of variables describing interception of a moving target: velocity of the target (v_t), velocity of the actor (v_a), heading angle of the actor (ϕ) relative to the allocentric reference direction, bearing angle of the moving target (ψ) relative to the same allocentric reference direction, and the difference between these two angles, which is the target-heading angle ($\beta = \psi - \phi$). (b) The CTH strategy with its associated constraint. (c) The pursuit strategy with its two associated constraints. (d) The CB strategy with its three associated constraints.

The constant target-heading, pursuit, and constant bearing strategies

Ample previous research has investigated how humans intercept a moving target in a wide variety of different tasks using different experimental paradigms. Based on the different observations made in these experiments, researchers have proposed three strategies to describe human locomotor interception: the constant target-heading strategy (CTH), the pursuit strategy, and the constant bearing strategy (CB). To illustrate these three strategies, consider a basic scenario in which an actor steers to intercept a moving target as depicted in Figure 1a. Here, the bearing angle (ψ) is defined as the angle between the direction from the actor toward the target and a reference direction in space, which is some allocentric axis in the environment. The heading angle (ϕ) is the actor's direction of locomotion relative to the same allocentric reference axis, and the target-heading angle is the difference between these two angles ($\beta = \psi - \phi$). Thus, the target-heading angle is the angular deviation of the target from the actor's current direction of locomotion. The three interception strategies can now

be described in terms of these angles and their rate of change over time during interception.

The different strategies can be conceptualized by considering which of the involved angles are constrained throughout interception. In the most general case, the CTH strategy, the actor is observed to keep the target-heading constant at some arbitrary value throughout interception ($\dot{\beta} = 0$; see Figure 1b). Therefore, this strategy usually results in a curved interception path. Second, if during steering the target-heading angle is constant but additionally constrained to a value of zero ($\beta = 0$ and $\dot{\beta} = 0$; see Figure 1c), one obtains the pursuit strategy, which again usually results in curved interception trajectories. Finally, according to the CB strategy, the actor additionally steers in such a way that the target's bearing angle is also constant ($\dot{\psi} = 0$). Such steering results in a straight interception path; i.e., the heading is constant ($\dot{\phi} = 0$). Although extensions of the CB strategy have been proposed that allow for initially curved paths (Fajen & Warren, 2007) due to inertia, these models also predict straight paths after a brief period. Because the target-heading is the difference between the target's bearing and the heading, both of which are constant throughout interception, the target-heading is also constant in this case ($\dot{\beta} = 0$;

see Figure 1d) as in the previous two interception strategies. Thus, both the CB strategy and the pursuit strategy are special cases of the CTH strategy.

How can one find out which strategy best describes human interception behavior? A first step in providing an answer to this question is to analyze the above angular quantities during human interception tasks. The CTH strategy can be distinguished from the CB strategy in two ways. First, whereas the CB strategy depends on the availability of a stable allocentric reference direction, the CTH strategy does not.¹ Second, whereas the CB strategy predicts a straight interception path, the CTH strategy is consistent with a range of interception paths with different degrees of curvature, including straight paths. The degree of curvature of a single trajectory when considering the CTH strategy is determined by the constant value of the target-heading angle. For example, the actor can produce a curved path when adopting a small target-heading angle as in Figure 1b, but the actor can also produce a straight path with a slightly larger constant target-heading angle as in Figure 1d. Thus, variability across trajectories may be a key factor in finding out which strategy best describes human interceptions.

A second important step in finding out which strategy humans use is the choice of the specific interception task because not all laboratory tasks allow distinguishing the above strategies. Previous research has predominately used two kinds of tasks: speed control tasks and steering control tasks. In the former task, actors intercept a moving target by adjusting their speed while moving along a fixed straight direction. Using this task, a number of studies have come to the conclusion that participants keep the target at a constant bearing angle (Bastin, Craig, & Montagne, 2006; Bastin, Jacobs, Morice, Craig, & Montagne, 2008; Chardenon, Montagne, Buekers, & Laurent, 2002; Chardenon, Montagne, Laurent, & Bootsma, 2004, 2005; Lenoir, Musch, Janssens, Thiery, & Uyttenhove, 1999; Lenoir, Musch, Thiery, & Savelsbergh, 2002). However, constraining participants' movements to follow a straight path prevents participants from moving directly toward the target and, therefore, prevents them from being able to use the pursuit strategy. Moreover, because participants cannot change their heading direction in this task and the target-heading is the difference between the target's bearing and the participant's heading ($\beta = \psi - \phi$), the target-heading angle covaries with the target's bearing. Therefore, observing interception behavior that is consistent with the CB strategy in a speed control task is also consistent with the CTH strategy. Thus, it is fundamentally not possible to distinguish the CB strategy from the CTH strategy based on the observed angular measurements when using speed control tasks.

In the second type of tasks, which use steering control, participants intercept a moving target mainly by directional steering adjustments. When steering on foot to intercept a moving target, Rushton et al. (1998) observed that participants walked directly toward the target. Such steering kept the target-heading angle close to zero throughout interception, consistent with the pursuit strategy. However, the target moved at a comparatively low speed of about 1°/s at the beginning of a trial in their study. When walking to intercept a faster target moving at about 8°/s at the beginning of a trial, Fajen and Warren (2004) reported that participants steered by heading in a direction 10° to 20° ahead of the target's current position, resulting in a target-heading greater than zero, inconsistent with the pursuit strategy. Complicating matters, the target-heading angle in the latter study was observed to stay constant in some conditions, whereas it continuously changed in other conditions. Specifically, target-heading was roughly constant in one condition if the target initially appeared on either side of the participant and subsequently moved across the participant's initial heading direction. But the target-heading angle continuously increased in a second condition in which the target initially appeared directly in front of the participant and subsequently moved outward to either side. Therefore, the study did not provide converging evidence for the CTH strategy.

Furthermore, Fajen and Warren's (2004) study did not reveal converging evidence for the CB strategy either. The authors reported the mean interception paths in their first experiment, but although some of the paths appeared quite linear, others appeared curved to different degrees. The authors did not report the target's bearing angles. Note that, in their study, the target initially appeared 3 to 4 m away from the participant and participants' walking speeds ranged from 1.1 to 1.3 m/s, which resulted in comparatively short interception durations. With short interception durations, the actor might have completed an interception before bringing any of the angular variables to a constant value, considering the inertia in human locomotion (e.g., see Fajen & Warren, 2003, 2007). In summary, studies investigating human locomotor interception with tasks involving steering control have reported data that neither provide convergent evidence for a single consistent strategy nor clear evidence for consistent switching between strategies.

Gaze and head directions during interceptive steering

Although ample research has investigated whether steering direction in locomotor interception can be described by the abovementioned three strategies based

on current visual information about target motion, it has been studied less how eye and head directions are coordinated to acquire visual information during interceptive steering. It has been shown that actors' gaze is predominantly anchored on the target during both manual interception (e.g., Brenner & Smeets, 2011; Cesqui, Mezzetti, Lacquaniti, & d'Avella, 2015; Lopez-Moliner & Brenner, 2016) and locomotor interception (e.g., McBeath, Shaffer, & Kaiser, 1995; Oudejans, Michaels, Bakker, & Davids, 1999; McLeod, Reed, & Dienes, 2006; Postma, den Otter, & Zaal, 2014). Specifically, to catch a fly ball in a short duration between 1.8 and 2.5 s, actors visually track the ball most of the time (Oudejans et al., 1999; Postma et al., 2014). Interestingly, a recent study in highly trained cricket players has suggested that batters coupled the rotation of their head to the movement of the ball while gaze anticipated the ball's position (Mann, Spratford, & Abernethy, 2013). Some studies have investigated gaze when steering a car along a road and found evidence for gaze being directed toward the tangent point of a curved road (Land & Lee, 1994), but others found evidence for gaze being directed in the direction that participants wanted to steer (Wilkie, Kountouriotis, Merat, & Wann, 2010). Overall, most studies on locomotor interception of moving targets have reported that subjects continuously track the target most of the time with smooth pursuit eye movements, reasoning that this pattern of behavior facilitates picking up current information and reducing uncertainty about the target's motion, which contributes to successful guidance of locomotor interception.

One concern in studying visually guided locomotor interception is that some experimental designs allow subjects to utilize cues or information beyond the actual observation of the target to guide their steering behavior. One possibility is that, because of a blocked design and a small number of conditions, subjects are able to learn the timing of interceptive steering. A second possibility is that subjects may utilize internal models, which they have acquired over longer time scales. Specifically, when intercepting a moving target, subjects may be able to extrapolate the target's trajectory. Such a strategy has been named the trajectory prediction (TP) strategy (see Saxberg, 1987). According to the TP strategy, initial observation of the target's movement allows subjects to predict the trajectory well enough so that they can predict where and when they can catch the target. Because the TP strategy for locomotor interception is carried out based on predictions about the target's future trajectory, systematic predictive eye movements or off-line tracking in locomotor interception could be regarded as evidence for the TP strategy. In the following paragraphs, we review and discuss relevant literature on potential sources of information beyond observational data in the context of visuomotor interception.

In a wide variety of visuomotor tasks, humans have been shown to be able to utilize predictive strategies because of learnt regularities. A prime example are predictive saccades during manual interception tasks. For example, when manually hitting an approaching fly ball, actors usually anticipate the ball's motion and direct their gaze at a point on the ball's future path (Diaz, Cooper, Rothkopf, & Hayhoe, 2013; Hayhoe, McKinney, Chajka, & Pelz, 2012; Hayhoe, Mennie, Sullivan, & Gorgos, 2005; Land & McLeod, 2000). Such anticipatory eye movements are observed even after the ball is visually occluded for a short duration (Diaz, Cooper, & Hayhoe, 2013). It has been proposed that an internal model of the target's trajectory is utilized to predict the target's future trajectory and make predictive eye movements or other actions (see Zago, McIntyre, Senot, & Lacquaniti, 2009 for a review; but also see Zhao & Warren, 2015).

Predictive gaze strategies have also been observed for smooth pursuit eye movements. It has been reported that actors can track a moving target with their eyes even after the target is visually occluded, and this off-line tracking is usually performed through a combination of smooth pursuit and saccades (Bennett & Barnes, 2006; Bennett, Orban de Xivry, Barnes, & Lefèvre, 2007; Fookien, Yeo, Pai, & Sperling, 2016; Orban de Xivry, Missal, & Lefèvre, 2008). These findings could also imply that an internal model of the target's trajectory is used to guide off-line tracking. Nevertheless, such predictive tracking is contingent on subjects having learnt about the regularities of targets' trajectories, e.g., in a blocked design or other cognitive factors (Barnes, 2008).

For the interception durations in the current experiments, the TP strategy is the most relevant alternative explanation of visuomotor interception behavior. But empirical evidence for the TP strategy in interception tasks exceeding a few seconds is scarce. For example, it has been shown that even skilled baseball players cannot accurately estimate a fly ball's trajectory, which challenges the TP strategy (Shaffer & McBeath, 2005). Fink, Foo, and Warren (2009) examined locomotor interception by asking participants to walk to catch a fly ball in a virtual environment like an outfielder in a baseball game. They showed that, when the fly ball's trajectory was perturbed midway in a trial, participants adjusted their locomotion in response to the ball's new trajectory. Recently, Zhao and Warren (2017) asked participants to walk to intercept a target moving on the ground in a virtual environment. In this task, the target was blurred to varying degrees in the midst of a trial. Subjects' interception accuracy and precision progressively decreased significantly with lower visibility. Overall, these findings strongly suggest a crucial dependence of locomotor interception on the availability of current

information and that tracking the target with gaze is a reliable indication of the online control of locomotor interception.

The current study: Steering, gaze, and head directions during interception

Taken together, previous empirical findings do not provide converging evidence for a single interception strategy or a single gaze strategy. In the current study, we investigated human visuomotor interception by asking participants to steer a car to intercept a moving target in a virtual environment. Based on our analysis of previous studies, we designed the task such that participants were neither constrained to stay on a linear path nor constrained by the spatial layout as the virtual environment was very large with respect to possible interception trajectories. Furthermore, we designed the task in such a way that interceptions usually lasted longer than 6 s so that the angular variables relevant for distinguishing the pursuit strategy, the CTH strategy, and the CB strategy as depicted in Figure 1 could be investigated more easily. To encourage subjects to use online information about the targets' motion and reduce the predictability of the targets, we used a randomized design with three different target velocities. By analyzing the angular variables of steering, we investigated which of the three strategies best describes human visuomotor interception in this task.

Because we were interested in the online control of interceptive steering, we also investigated how participants coordinated their gaze and head movements during steering as both are known to be coordinated in natural behavior (Guitton, 1992; Land & Lee, 1994). To this end, we defined gaze and head angles relative to the direction of the car's heading and to the direction toward the target (see Figure 2). Although the design of our experiment encouraged participants' use of online information and avoided increased predictability of targets' trajectories by randomizing the targets' velocities, it is not possible to exclude predictive strategies altogether. Specifically, subjects may have used the TP strategy. To investigate whether subjects relied on online observations or on the TP strategy, we introduced a condition in which the target was occluded 2.5 s after its appearance in the scene. This occlusion condition allowed investigating interception strategies as well as gaze behavior when no online information about the target's position was available.

In the visible conditions, the pursuit, CTH, or CB strategies may be preferable because they allow for continuous corrections in steering. By contrast, in the occlusion condition, the TP strategy might be preferable because initial visual information about the target's motion could be used to extrapolate and make

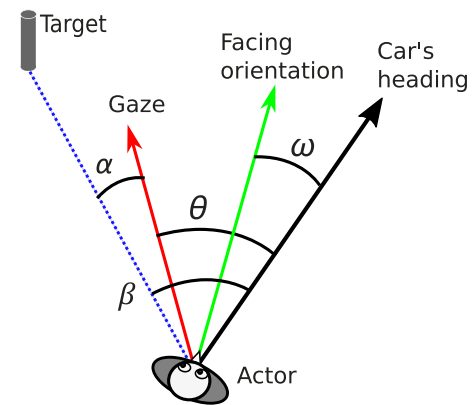


Figure 2. Definition of gaze and head angles during interception. The angle between the gaze direction and the direction toward the target is the gaze–target angle (α). The angle between the gaze direction and the car's heading is the gaze–heading angle (θ). Finally, the direction between the head orientation and the car's heading is the facing orientation (ω). The target–heading angle (β) is the angle between the direction to the moving target and the direction of the actor as defined in Figure 1.

predictions about its future trajectory. However, if occlusion of the target results in subjects' inability to successfully track and intercept the target, we can conclude that online information about the target's position is necessary for interception. In the occlusion condition, we distinguish two types of predictive strategies, which can be differentiated based on gaze behavior. Either participants predict an interception location and then anchor their gaze there and steer toward this location or participants may continue to track the target even after it is occluded. The former strategy suggests that, after target occlusion, subjects may saccade to the predicted interception location, which, in the present experimental design, is located to the right side of the heading direction. Maintaining gaze there, subjects may make hardly any additional saccades, similar to gaze anchoring (Neggers & Bekkering, 2001). The latter strategy instead suggests that after the target's occlusion, subjects' gaze may target a series of predicted locations along the target's path. This would lead participants to carry out small amplitude saccades similar to those observed in studies investigating off-line visual tracking (e.g., Bennett & Barnes, 2006; Bennett et al., 2007).

Methods

Participants

Eighteen students (12 females, six males; 18–36 years old) at the Institute of Psychology participated in this

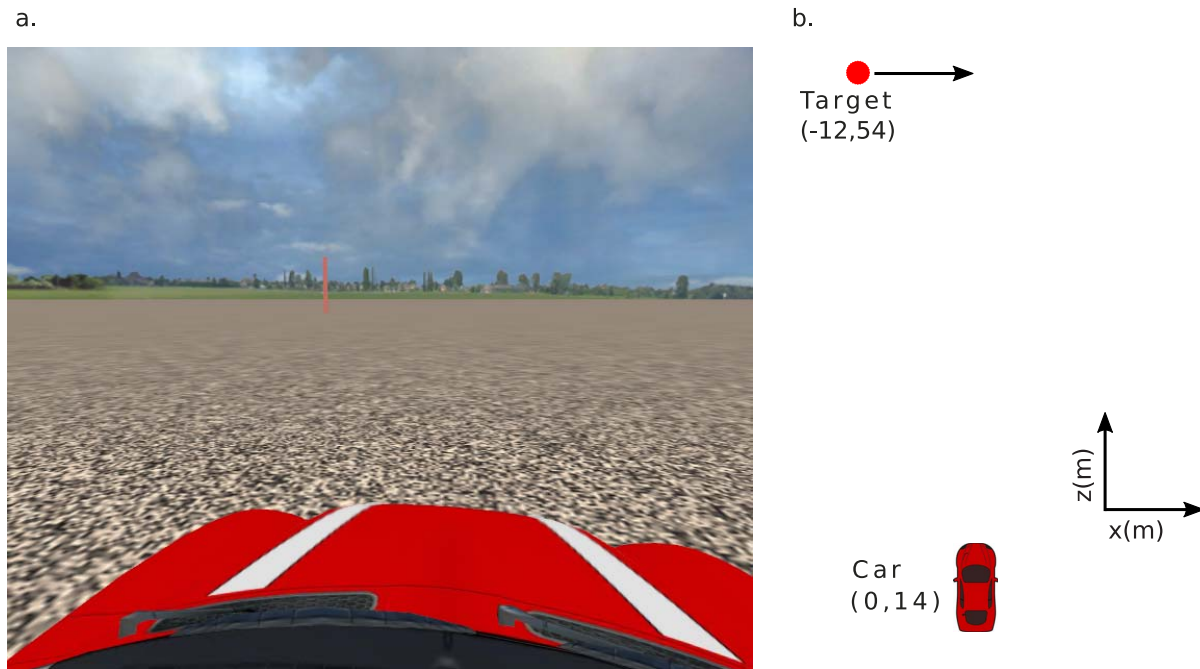


Figure 3. Experimental stimuli and virtual scene layout. (a) A representative view of the experimental scene from the perspective of a participant at the moment when the target appears. (b) Top view of the virtual environment's layout, including the car and target at the moment when the target appears.

experiment. They all had a driver's license and had normal or corrected-to-normal vision. They read and signed the informed consent form prior to carrying out the experiment and received course credit for their participation.

Apparatus

The virtual environment was generated on a Dell workstation with Vizard software (WorldViz, Santa Barbara, CA) and presented in a head-mounted display (HMD; Oculus Rift DK 2, OculusVR, Irvine, CA), which provided stereoscopic viewing with an 80° (vertical) \times 80° (horizontal) field of view. An SMI eye tracker was integrated in the HMD, which was calibrated and programmed through the eye-tracking HMD software package (SMI, Teltow, Germany). Participants sat in a chair in front of a desk on which a force feedback steering wheel was fixed (Driving Force GT, Logitech, Newark, CA). The chair was positioned in alignment with the steering wheel. Participants wore the HMD and used the steering wheel to steer a car in the virtual environment. The steering wheel had a turning range of 450° left/right. The ratio of the current turning rate of the car was fixed to the angle of the steering wheel at $1^\circ/\text{s} : 5^\circ$ to balance between precision and efficiency of steering. The car's current heading angle, i.e., its orientation with reference to an allocentric reference axis, was updated by integrating

the turning rate of the car during each frame:

$$\varphi_{i+1} = \varphi_i + \Delta t_i \dot{\varphi}_i, \quad (1)$$

where φ_i is the heading angle in the i th frame, $\dot{\varphi}_i$ is the turning rate, and Δt_i is the duration of a single frame, respectively. The car always moved at 7 m/s, and its location was updated during each frame by translating it along its current heading direction by the distance it traveled during that frame ($7\Delta t_i$ m). Updating of the display and data recording were synchronized at 30 Hz.

The participants' viewpoint was initially placed at the center of the car's traverse plane with a height of 1.4 m from the ground; its orientation was aligned with the car. With this setup, participants viewed the environment through the car's windshield as they sat in the chair and looked straight ahead. Additionally, participants could move their head freely during steering, and at every time step, the viewpoint was updated with the car's as well as the HMD's translation and rotation, and the display was updated accordingly (see Figure 3a for an example display). Thus, we provided a naturalistic visual experience similar to everyday driving.

Displays

The virtual environment was a round arena with a radius of 300 m, consisting of a ground plane with a

random noise texture, a blue sky-dome with clouds, and a surrounding background image showing vegetation at the edge of the arena (Figure 3a). We set the center of the arena as the origin of the environment ($x = 0$, $z = 0$ m). The target was a red textured cylinder, 3 m tall with a radius of 0.2 m. The car was 3.6 m long, 1.8 m wide, and 1.5 m tall. At the beginning of each trial, the car appeared at the origin ($x = 0$, $z = 0$ m), facing in the z direction, and immediately began moving straight ahead along a green strip (14 m long) on the ground. At the end of the strip ($x = 0$, $z = 14$ m), the target appeared 40 m ahead and 12 m to the left of the car ($x = -12$, $z = 54$ m, i.e., 16.67° with reference to z -axis) and immediately began moving rightward on a path parallel to the x -axis (Figure 3b). Participants steered the car to intercept the target. The initial location and the moving direction of the target were mirrored left and right about the z -axis in a counterbalanced fashion, and data were collapsed in the analysis. In half of the trials, the target was visible throughout interception, and in the other half of the trials, it was visually occluded 2.5 s after having appeared. A trial ended as soon as the target was within 1.8 m from the car's center, corresponding to an interception, or the car went beyond the line $z = 54$ m, corresponding to a miss. To prevent a potential influence of landmarks on interception, the surrounding background image and the sky were rotated by an angle chosen uniformly at random between 0° to 270° for each trial.

Design and procedure

Three target speeds (4, 5, or 6 m/s) and two target visibility levels yielded a 3×2 factorial within-participant design with six target conditions. Each target condition was repeated 16 times, yielding 96 trials for each participant. The order of the trials was randomized. At the beginning of each experimental session, participants sat in front of the desk and tried turning the steering wheel left and right a couple of times. Then they put on the HMD, and the eye tracker was calibrated. After calibration, subjects intercepted four targets for each of the six conditions yielding 24 practice trials followed by the 96 experimental trials. All participants were instructed to intercept the targets as accurately and quickly as possible. An experimental session lasted approximately 40 min.

Steering analysis

Because the car was the end effector and participants could move their head freely, we used the car's position and orientation for steering analysis. Because the virtual car was 3.6 m in length, we defined a trial as a

successful interception if the center of the car reached a distance less than 1.8 m to the target. Interception duration spanned from the moment the target appeared to the end of the trial, i.e., successful interception according to the above criterion. We defined the x direction as the allocentric reference axis and computed the target's bearing relative to it in each frame according to the following equation:

$$\psi_i = \operatorname{arccot}[(X_i - x_i)/(Z_i - z_i)], \quad (2)$$

where (X_i, Z_i) and (x_i, z_i) are the coordinates of the target and the car, respectively, in the i th frame. As heading direction of the car was recorded in each frame (φ_i on the i th frame), the target-heading in the i th frame is computed as $\beta_i = \psi_i - \varphi_i$. To compute the absolute rate of change of these angles, we divided their absolute difference between two successive frames by the time passed between those two frames.

When the car reached the vicinity of the target, the target's bearing angle and target-heading angle usually rose or fell quickly as reported in previous studies due to the short distance between the car and the target (e.g., Lenoir et al., 1999). To eliminate this quickly changing angular data, we excluded all data after the center of the car reached a distance of 3.6 m to the target from further analysis in each trial. For the remaining data, we computed mean time series of interception path (the x and z positions) as well as mean time series of target-heading (φ), bearing (ψ), and their absolute rate of change, respectively.

To compare the angular quantities across multiple trials and multiple participants, one needs to normalize the respective time series because of individual trials' varying durations. As in previous studies, the time series of angular quantities, such as target-heading angle, was normalized to unit length for each participant for each condition. Subsequently, the time series were binned into 50 time bins, and the mean of each variable was computed bin-wise across trials, yielding the mean normalized time series for each condition. When considering deviations from zero in the following analyses, absolute values of the time series were computed to avoid averaging positive and negative values to zero. The normalized mean time series of the other angular quantities were obtained analogously.

Eye movement analysis

At the beginning of each experimental session, the participant put on the HMD and adjusted it for comfortable wearing. The SMI eye tracker was calibrated using a nine-point calibration grid. Calibration accuracy was measured as the mean distance between the participant's fixation point to each calibration point at the four corners. The mean

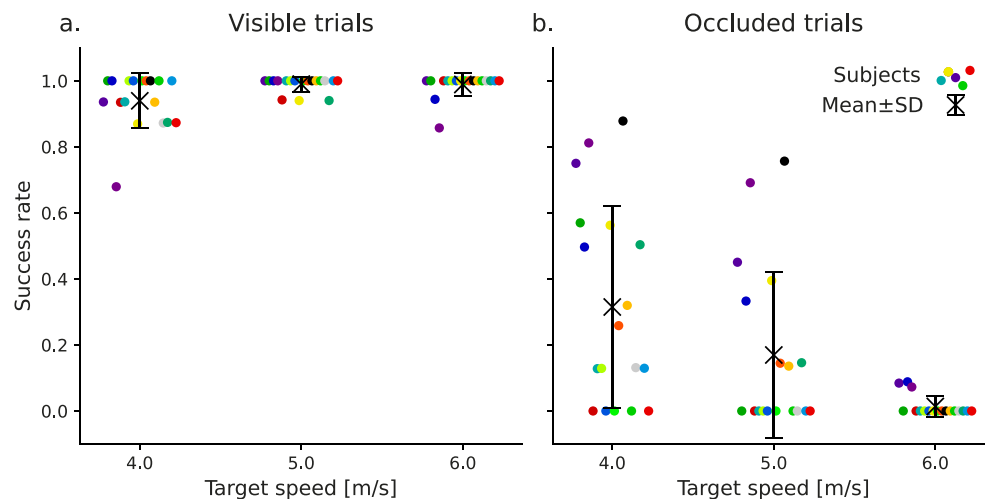


Figure 4. Each participant's interception rate for visible and occluded targets. (a) The left panel shows the interception rate of visible targets for all subjects in conditions with progressively higher target speeds of 4, 5, and 6 m/s. (b) The right panel shows the corresponding interception rates for the occluded condition for the same speeds. The color-coding is maintained consistently throughout all figures to identify individual differences between subjects.

calibration accuracy was 0.51° ($SD = 0.20^\circ$) across participants. Within the Vizard software, the 3-D gaze unit vector with reference to the participant's head was read online from the SMI software package. For each frame, this gaze vector as well as position and orientation of the participant's head with respect to the environment were recorded. During analysis, we combined the gaze unit vector with the participant's head position and orientation to calculate the 3-D gaze direction in the environment.

Subsequent analysis identified gaze shifts based on 3-D gaze angular velocity. To compute gaze angular velocity, we divided the difference between two successive gaze vectors by the duration between them. The resulting time series of gaze velocity was subsequently filtered with a three-unit-wide median filter. We identified saccades as local maxima of the filtered velocity with a value higher than $50^\circ/\text{s}$. Because our data was recorded at a rather low frequency of 30 Hz, we found that the following processing resulted in better identification of the start and end of a saccade. We applied a 7-unit-wide kernel $[-0.5, 0, 0.5, 1.0, 0.5, 0, -0.5]$ to the filtered gaze velocity signal. Such filtering produced exaggerated valleys in the gaze velocity signal just before and after a maximum (see similar filtering in Diaz, Cooper, Kit, & Hayhoe, 2013). Then we computed the time series of gaze acceleration by differencing the filtered gaze velocity signal. Based on this processing pipeline, we identified the first frame with a local maximum in acceleration signal prior to the local maximum in velocity (greater than $50^\circ/\text{s}$) as the start of the saccade and the first frame with a local minimum in acceleration signal after the local maximum in velocity as the end of the saccade. The saccade amplitude was computed as the angle between the two

3-D gaze vectors at the start and end of the saccade. Due to the low frequency of data collection, we could not discriminate between signal noise and a saccade whose duration was shorter than two frames (67 ms). Therefore, we excluded potential saccades shorter than 67 ms from further analysis.

Results

Interception performance

We first analyzed participants' interception performance to examine how target visibility influenced their ability to successfully intercept the moving targets. Because of the individual differences, we first show each participant's interception rate in both target conditions separately for each velocity in Figure 4. As expected, the interception rates for occluded targets are clearly and significantly lower than those for visible targets. For visible targets, the mean interception rate across participants is 0.94 ($SD = 0.08$) for target speed 4 m/s, 0.99 ($SD = 0.02$) for 5 m/s, and 0.99 ($SD = 0.03$) for 6 m/s; for occluded targets, it is 0.31 ($SD = 0.31$) for 4 m/s, 0.16 ($SD = 0.25$) for 5 m/s, and 0.01 ($SD = 0.02$) for 6 m/s. A two-way, repeated-measures ANOVA on interception rate indicated significant main effects of target visibility, $F(1, 17) = 289.17$, $p < 0.01$, $\eta_p^2 = 0.94$, and target speed, $F(2, 34) = 10.13$, $p < 0.01$, $\eta_p^2 = 0.37$, with a significant interaction between them, $F(2, 34) = 19.14$, $p < 0.01$, $\eta_p^2 = 0.53$. A follow-up simple effect test with Sidak adjustment revealed a significant main effect of target speed for both visible targets, $F(2, 16) =$

10.99, $p < 0.01$, and occluded targets, $F(2, 16) = 4.56$, $p < 0.05$. The significant main effect of target visibility indicates that target occlusion severely impaired interception performance. The significant interaction confirms that participants intercepted faster targets slightly more than slower targets when targets were visible; by contrast, they intercepted fewer faster targets than slower targets when targets were occluded. Thus, these results show that subjects indeed relied heavily on the visibility of the targets during interception in our experiments, confirming that our experimental setup did indeed investigate primarily online control of interceptive steering.

Individual differences in interception rate are particularly apparent for slower occluded targets (4 or 5 m/s). Although some participants missed most of the slower occluded targets, seven participants intercepted more than half the targets. For example, participants using higher turning rates (data plotted in blue and violet) intercepted about 80% of slower occluded targets. Nevertheless, this pattern of steering was not sufficient for them to intercept the majority of occluded targets at the fastest speed as the violet participants missed most of the targets traveling at a velocity of 6 m/s as did all the other participants. Because long interception durations may be important for the interception strategies to fully reveal themselves through the angular variables, we report participants' interception durations here. For visible targets, the mean interception duration is 6.19 s ($SD = 0.12$) for target speed 4 m/s, 7.52 s ($SD = 0.37$) for 5 m/s, and 12.17 s ($SD = 1.08$) for 6 m/s; for occluded targets, it is 5.82 s ($SD = 0.23$) for 4 m/s, 6.14 s ($SD = 0.47$) for 5 m/s, and 6.61 s ($SD = 0.85$) for 6 m/s. These analyses confirm that interception durations were longer in the current study compared to most previous studies on visuomotor interception.

Strategy for intercepting visible targets

To investigate which of the three proposed strategies best describes the interception behavior in our experimental setup, we examined participants' angular variables according to the way these have been described in the literature as depicted in Figure 1. First, we computed each participant's mean time series of the target-heading and the bearing angles as well as their respective rates of change. Figure 5a shows each participant's data represented by individual colors across target speeds, and the rates of change of the target-heading and bearing angles are shown in Figure 5b. The CB strategy requires the rates of change of the bearing, heading, and target-heading angles to be close to zero. The bearing angle's absolute rate of change was significantly different from zero (one-sample t test

against zero), $t(53) = 31.59$, $p < 0.001$, $d = 4.30$, across all speeds in the visible trials with a mean of $8.80^\circ/\text{s}$ ($SD = 2.05^\circ/\text{s}$) and a 95% confidence interval of [8.26, 9.35]. Similarly, the absolute rate of change of the heading angle, i.e., the absolute turning rates in the visible conditions were significantly different from zero, $t(53) = 43.12$, $p < 0.001$, $d = 5.87$, with a mean turning rate of $8.91^\circ/\text{s}$ ($SD = 1.52^\circ/\text{s}$) and a 95% confidence interval of [8.51, 9.32]. Thus, according to these results, the CB strategy is not a good account of subjects' behavior in our experiments.

Furthermore, the target-heading angle can be used to distinguish between the pursuit and the CTH strategies. The pursuit strategy would lead to a target-heading angle of zero during interception. At the moment of target appearance, although participants still moved straight ahead, the slowest targets moving at 4 m/s resulted in a rate of change in the target-heading at about $5.7^\circ/\text{s}$, whereas the fastest target moving at 6 m/s resulted in a rate of change in the target-heading of about $8.5^\circ/\text{s}$. But during interception, the mean target-heading angle in our experiments was 16.60° ($SD = 5.64^\circ$) with a 95% confidence interval of [15.10, 18.11]. Accordingly, a one-sample t test against a mean of zero showed that the target-heading angle was significantly, $t(53) = 21.64$, $p < 0.001$, $d = 2.95$, different from zero. Taken together, the above results suggest that neither the CB nor the pursuit strategy can describe subjects' interception in our experiment.

The only strategy left is the CTH, which has only a single constraint, which is that the rate of change of the target-heading angle is close to zero. We first analyzed the mean of the absolute rate of change, which was $3.07^\circ/\text{s}$ ($SD = 1.07^\circ/\text{s}$) with a 95% confidence interval of [2.79, 3.36]. This is significantly different from zero, as the one-sample t test against zero was significant, $t(53) = 21.15$, $p < 0.01$, $d = 2.88$. Noting that subjects adjusted their target-heading angle during the beginning of the interception, some deviation from zero of its rate of change is to be expected. In order to still differentiate between CTH and CB, we compared the absolute rates of change in target-heading and target's bearing by computing their means for each participant as depicted in Figure 5b. Specifically, we averaged the absolute rate of change over each trial, then computed the mean for each target speed. A paired t test indicated that the mean absolute rate of target-heading ($M = 2.97^\circ/\text{s}$, $SD = 0.89^\circ/\text{s}$) was significantly smaller than that of target's bearing ($M = 8.70^\circ/\text{s}$, $SD = 2.12^\circ/\text{s}$) across target speed, $t(53) = -15.57$, $p < 0.01$, $d = 2.12$. We additionally computed the confidence intervals of the final target-heading and bearing angles separately for the three speed conditions in the visible trials. Because of the experimental setup, the initial target-heading angle was 16.67° and the initial bearing angle was 106.67° at the moment when the target appeared. The

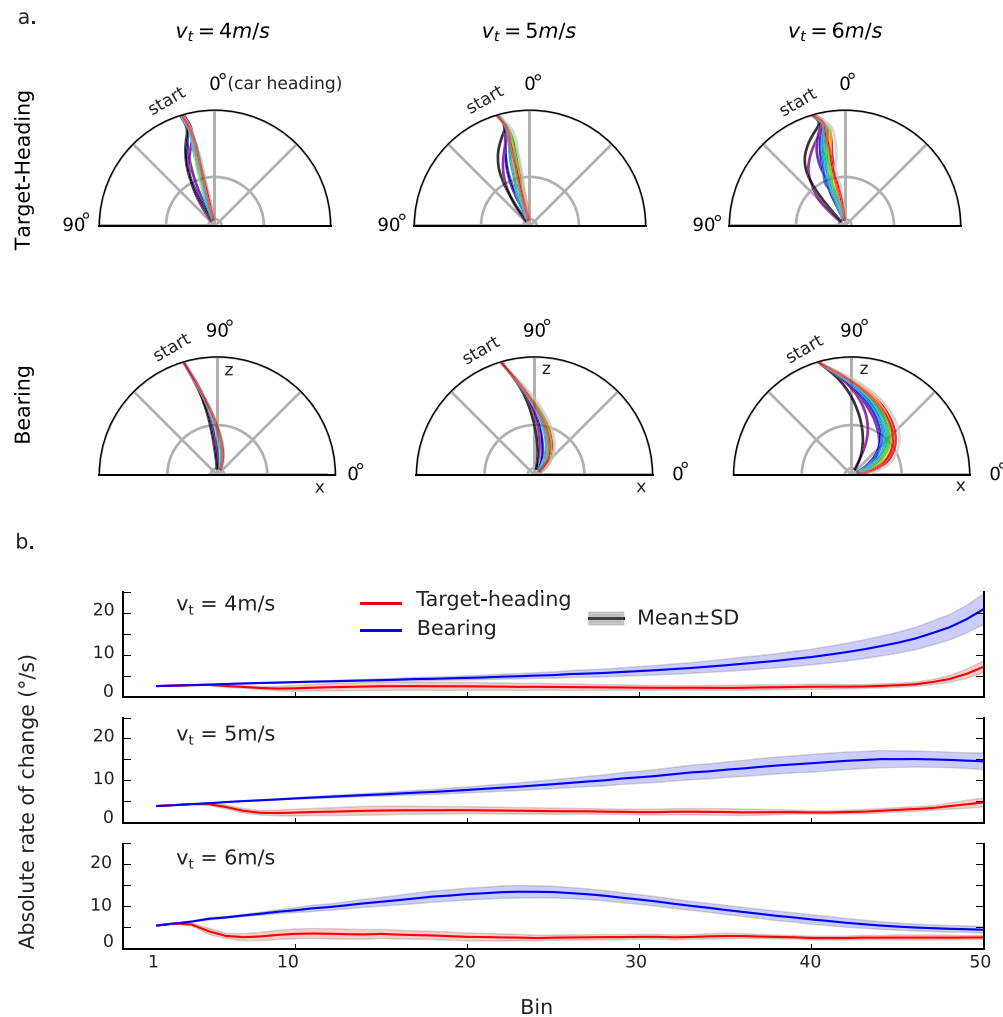


Figure 5. Target-heading and bearing angles and their rates of change. (a) Mean time series of target-heading and bearing angle in polar coordinates with each participant's data represented by the same color across target speeds. The outer circles represent the start of interceptions and inner circle 60% of the interception courses. The angular quantities are shown for individual subjects separately for the three different velocity conditions. (b) Mean time series of the absolute rates of change of the target-heading and the target-bearing angles across participants separately for the three velocity conditions. Shaded areas represent standard deviation across participants. The data were normalized to a duration of unit length and subdivided into 50 bins.

95% confidence interval of the final target-heading angle for a target speed of 4 m/s is $[14.264^\circ, 21.542^\circ]$; for a target speed of 5 m/s, it is $[16.249^\circ, 23.756^\circ]$, and for a target speed of 6 m/s, it is $[9.65^\circ, 20.607^\circ]$. By contrast, the 95% confidence interval of the final bearing angle for target speeds of 4 m/s is $[64.8^\circ, 75.9^\circ]$; for target speeds of 5 m/s, it is $[38.9^\circ, 51.8^\circ]$; and for target speeds of 6 m/s, it is $[14.2^\circ, 28.5^\circ]$. This means that the initial target-heading angle was within the 95% confidence interval of the final target-heading angle in all conditions, whereas this was not the case for the bearing angle in any of the three conditions. Thus, taken together, these results provide evidence that interceptive steering is better accounted for by the CTH strategy rather than the CB strategy or the pursuit strategy in the present experiments.

To further substantiate the above results, we analyzed the mean interception paths in all six conditions, which are shown in Figure 6 with each participant's mean path represented by the same color across target conditions. Additionally, the mean positions of the targets at the end of the trials for each participant are plotted. The mean trajectories show some variability across subjects with some participants consistently adopting higher turning rates (trajectories colored in violet and blue) than others. Therefore, we examined how stable individual participant's interception was in terms of their final target-heading. We computed steering variability as the SD of the final target-heading angle for each participant and then averaged them across participants for each target speed. The mean variability within participants was

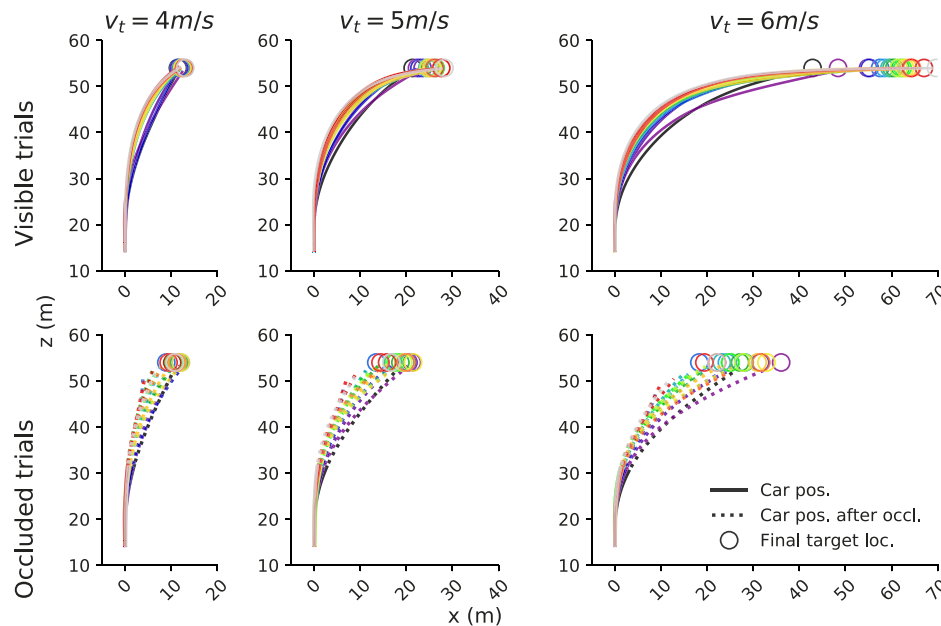


Figure 6. Mean interception paths and final target locations for all six experimental conditions and all participants. Each participant's paths are represented by the same color across target conditions. The final target locations for each participant are represented by open circles of the same color as the participant's paths. The paths here range from the beginning of a trial to the moment with shortest distance between the car and the target. Trajectories and final target locations were color-coded consistently with previous and subsequent figures. The upper row corresponds to visible targets, and the lower row corresponds to occluded targets. The three columns correspond to progressively higher target speeds of 4, 5, and 6 m/s.

6.35° ($SD = 2.12^\circ$) for target speed of 4 m/s, 7.54° ($SD = 3.08^\circ$) for 5 m/s, and 7.18° ($SD = 3.71^\circ$) for 6 m/s. A one-way, repeated-measures ANOVA indicated that target speed had no significant influence on variability within participants, $F(2, 34) = 1.77$, $p = 0.19$. These results indicate a stable pattern of steering within participants in terms of the CTH strategy regardless of target speed.

Eye and head movements during interception

We analyzed participants' eye and head movements to examine how behavior was coordinated to guide interception. In particular, we examined whether participants visually tracked the target for picking up current information or systematically made predictive eye movements, such as looking at a predicted interception location or used off-line tracking of occluded targets. Representative gaze directions of one participant from one visible and one occluded trial are illustrated in Figure 7. At the beginning of the trial, the participant looked in the heading direction. After detecting the target in the periphery, the participant made a saccade to the target and maintained gaze on it either until interception or until target occlusion. After the target was occluded as shown in Figure 7b, the participant directed gaze in the heading direction, then once looked back along the trajectory of the occluded

target. While the target was occluded, gaze mostly lagged behind the actual position of the occluded target. Subsequently, the participant made a saccade back toward the heading direction. Although the gaze and head directions in these two trials were representative of our subjects' behavior, the quantities describing head and gaze behavior across subjects on which subsequent statistical analyses are based are shown in Figure 8. Data show that, before shifting their gaze toward the target, subjects oriented their head and gaze (facing-heading and gaze-heading in Figure 2) approximately in the direction of the car's heading. Statistical analysis across participants for the facing-heading angle resulted in a mean of -0.137° ($SD = 0.61$) and a 95% confidence interval of $[-0.298, 0.0239]$, and the gaze-heading angle was, on average, about 2° off the heading direction toward the target with a mean of 1.91° ($SD = 1.79^\circ$) and a 95% confidence interval of $[1.43, 2.39]$ at the beginning of the trials.

Evidence for continuous target tracking

Gaze and head behavior during interception in the visible conditions was analyzed involving the respective angular quantities according to the definitions in Figure 2. Figure 8 shows the gaze and head angle time series separately for the three different velocity conditions in the visible trials only. In subplots a–c, we again used the same colors for individual participants so that the

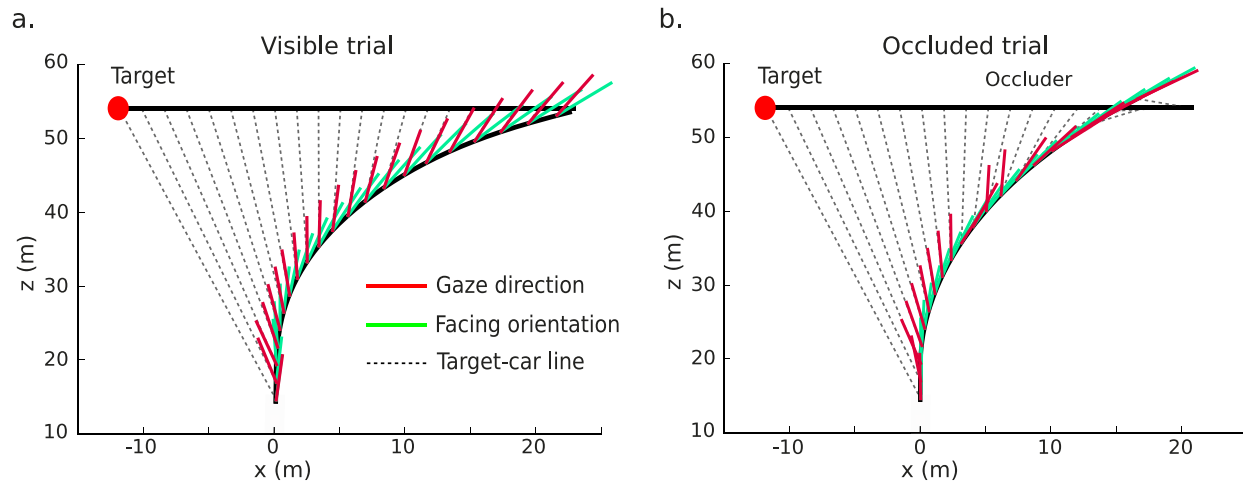


Figure 7. Eye and head direction during representative interception trials. (a) Interception trajectory together with the gaze direction (red) and the facing orientation (green) for a visible target and (b) an occluded target. The targets moved at 5 m/s.

variability in visual behavior across subjects can be appreciated. These data directly relate to the hypothesized interception strategies and allow a number of observations, which are corroborated in subsequent paragraphs through statistical testing. First, if subjects continuously used visual information about the target's position, they should maintain gaze on the target throughout interception, leading to a gaze-target angle α close to zero as depicted in Figure 8a. Second, if subjects used the CTH strategy and maintained gaze on the target, then gaze-heading angle θ as depicted in Figure 8b should be highly correlated with the steering direction, i.e., the target-heading angle β . Third, the overall gaze direction in space is the superposition of the actors' eye movements and their head and body orientation. Thus, based on previous studies about the coordination of eye and head movements, we expect the gaze-heading angle θ and facing-heading angle ω to be correlated (Guitton, 1992; Land & Lee, 1994; Mann et al., 2013). In the following section, we provide statistical tests for these hypotheses.

First, during interception of visible targets, the mean gaze-target angle α across participants was -2.51° ($SD = 1.15^\circ$) for target speed of 4 m/s with a 95% confidence interval of $[-3.04, -1.97]$, -2.72° ($SD = 1.59^\circ$) for 5 m/s with a 95% confidence interval of $[-3.45, -1.98]$, and -2.72° ($SD = 2.36^\circ$) for 6 m/s with a 95% confidence interval of $[-3.80, -1.63]$. To confirm that these values suggest a stable gaze behavior across participants, velocities, and conditions, we carried out a two-way, repeated-measures ANOVA on subject-wise mean gaze-target angles, which did not show a significant effect of target condition, $F(1, 17) = 0.51$, $p > 0.48$, nor a significant effect of target speed, $F(2, 34) = 2.48$, $p > 0.98$.

To further substantiate these results, we divided each trial into two segments: The first segment started

at the moment in which the target appeared and ended 2.5 s later when the targets were occluded in the occluded trials, and the second segment started directly after the first segment, that is, 2.5 s after the target's appearance. Figure 9a shows density functions of the gaze-target angle α over all participants. Targets were visible in both segments of visible trials and only visible during the first segment of occluded trials. The density functions of both segments again indicate that participants visually tracked the target most of the time. Indeed, the mean proportion of gaze falling within 5° to the left or to the right of the target was 81.1% ($SD = 9.3\%$) in the visible trials within the first 2.5 s. The density function in the second segment indicates that participants visually tracked the target most of the time also after they had observed the target's initial motion in the first segment with a proportion of gaze falling within 5° to the left or to the right of the target of 88% ($SD = 8.3\%$). The lower peak in the density in Figure 9a at about 17° to the right of the target direction for the first segment of both visible and occluded trials can be attributed to participants still looking in the heading direction at the moment of target appearance (see Figure 7) and shifting gaze with a brief delay. Combined with the results about interception strategies in the previous section, the results here suggest that participants visually tracked the target most of the time for picking up current information about target motion and used the CTH strategy to guide their interception.

Second, because participants' strategy was best described by the CTH, and they maintained their gaze on the target during interception, the gaze-heading angle θ should be closely related to the target-heading angle β . This was confirmed as the correlation between target-heading angle and gaze-heading angle was $r = 0.80$ ($p < 10^{-3}$) for 4 m/s, $r = 0.81$ ($p < 10^{-3}$) for 5 m/s,

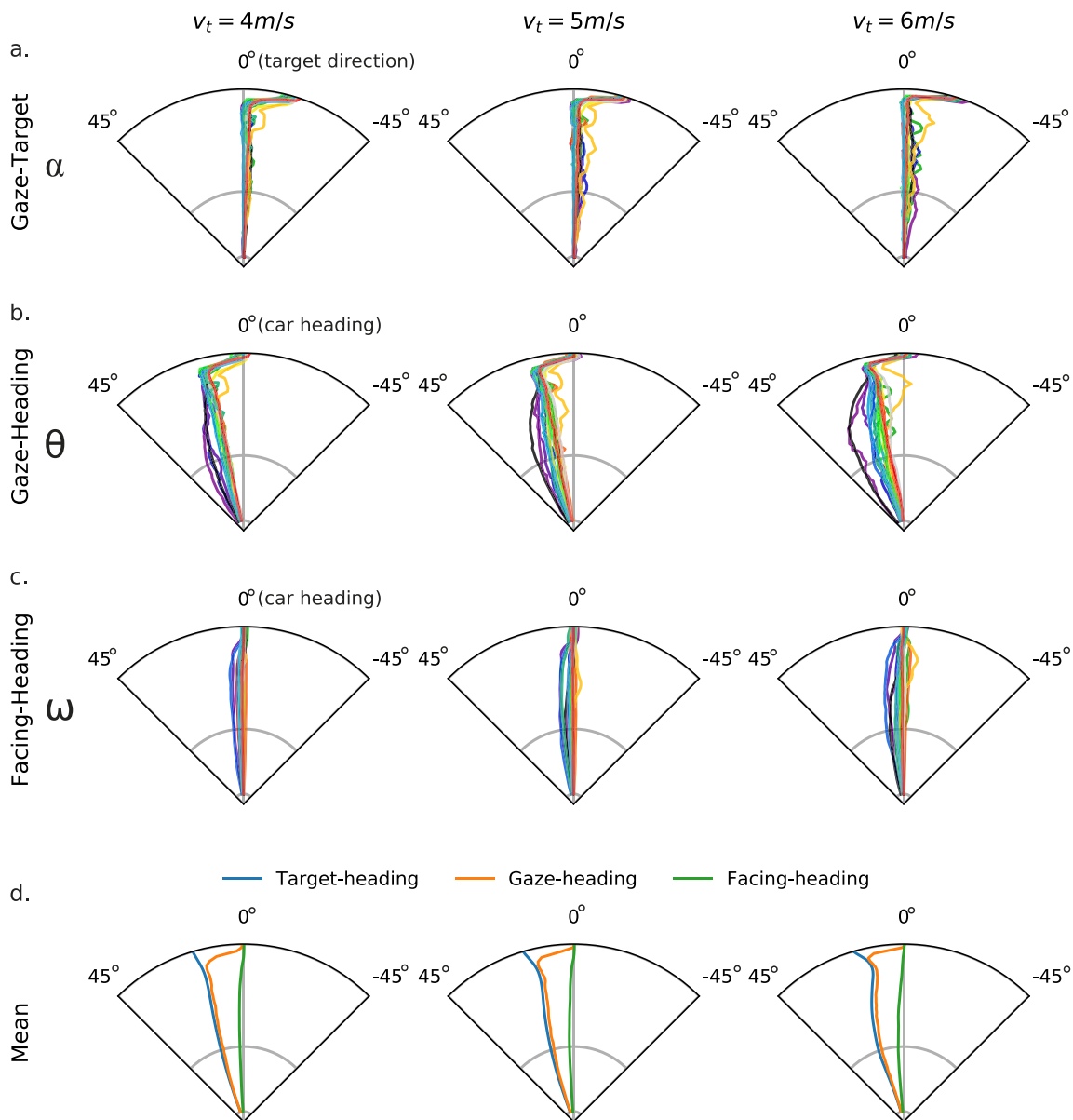


Figure 8. Head, gaze, and steering behavior of participants in the visible trials. Each participant's mean time series of gaze–target (a), gaze–heading (b), and facing–heading (c). (d) The grand mean time series of gaze–heading and facing–heading, averaged across participants, presented with that of target–heading.

and $r = 0.87$ ($p < 10^{-3}$) for 6 m/s. This is again evidence for the hypothesis that subjects tracked the target during interception and adjusted their gaze continuously in accordance with their steering to intercept the moving target. Note that this establishes a close connection between the direction in which subjects looked and the direction in which they steered.

Third, during interception of visible targets, participants' heads pointed, on average, slightly to the left side of the car's heading direction, i.e., toward the side that targets appeared. The mean facing orientation across participants was 2.28° ($SD = 2.71^\circ$) for target speed of 4 m/s, 2.73° ($SD = 2.59^\circ$) for 5 m/s, and 3.32°

($SD = 3.41^\circ$) for 6 m/s; in interception of occluded targets, it was 2.09° ($SD = 2.11^\circ$) for target speed of 4 m/s, 2.18° ($SD = 2.27^\circ$) for 5 m/s, and 1.70° ($SD = 2.78^\circ$) for 6 m/s. These results indicate that, in the interception of faster targets, participants oriented their head more toward the target when the target was visible than when it was occluded. To test whether gaze–heading θ angle and facing–heading angle ω were linked, we computed the correlation between the two angles for visible trials with a correlation coefficient of $r = 0.69$ ($p < 10^{-3}$) for 4 m/s, $r = 0.72$ ($p < 10^{-3}$) for 5 m/s, and $r = 0.81$ ($p < 10^{-3}$) for 6 m/s. Thus, gaze and head movements were closely coordinated to accomplish target tracking.

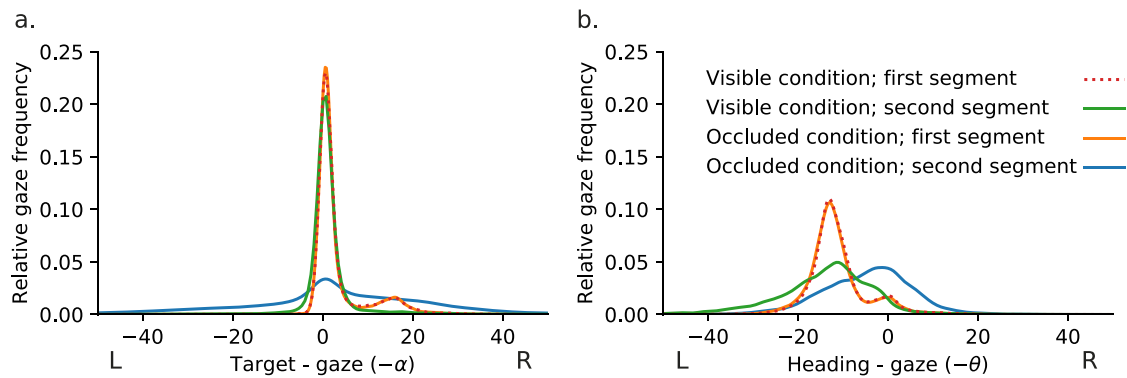


Figure 9. Relative gaze frequencies (kernel density estimates, bandwidth chosen according to Scott's rule) of the (a) gaze–target (α) and (b) gaze–heading (θ) angles. The negative of these angles is shown in this plot in order to facilitate interpretation: Negative angles mean that the subjects looked to the left of the target-heading direction and positive angles that they looked to the right. For both plots, the data were plotted separately for the first segment in the visible condition (dotted red) and the second segment in the visible condition (green) as well as the first segment in the occluded condition (orange) and the second segment in the occluded condition (blue).

Evidence for alternative visuomotor strategies

To exclude alternative hypotheses about possible predictive strategies, we examined participants' gaze shifts during interception. Specifically, although in the previous sections visuomotor behavior during visible trials was analyzed, we now compare gaze behavior between visible and occluded trials. The first row of Figure 10 shows the histograms of the number of saccades across all participants over the interception

duration in the visible trials. At the beginning of a trial, participants usually looked ahead in the initial heading direction; after they detected the target, they made saccades toward the target, which led to a large number of saccades within the first 0.5 s of interception maneuvers. After that, participants tracked the target with smooth pursuit most of the time and made saccades occasionally during the second trial segment across participants and target speed. When getting close to the target right before interception, the

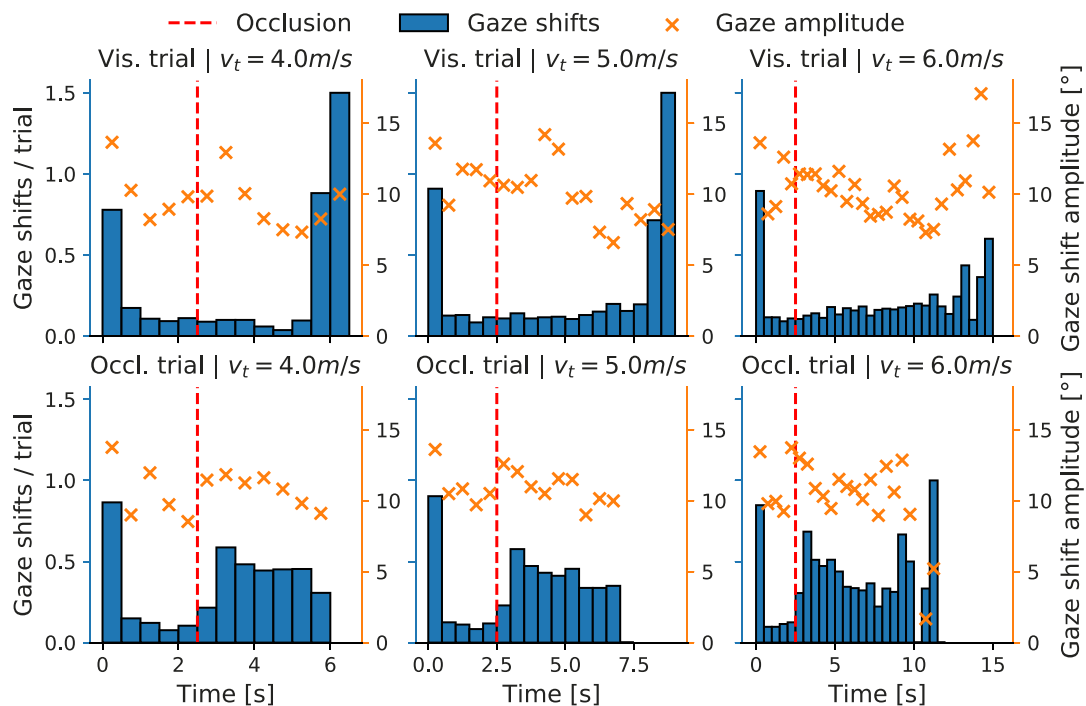


Figure 10. Histograms of gaze shifts per trial plotted along with the mean gaze shift amplitudes. The data were grouped into 0.5-s bins and averaged across trials in 0.5 s for both quantities. The red dashed lines mark 2.5 s (the time of target occlusion), which divides a trial into two segments. Top row: visible trials. Bottom row: occluded trial.

frequency of saccades increased again, which is attributable to the quickly changing target-heading angle. Therefore, toward the end of the interception, participants might make more saccades to maintain gaze on the target. The first row of Figure 10 also shows the mean saccade amplitudes over the interception duration across participants (see the orange \times symbols in the first row of Figure 10). At least three differences between visible trials and occluded trials can be discerned and linked to the continuous tracking, interception location prediction, and off-line tracking hypotheses. First, while the target was occluded, participants carried out a larger number of saccades compared to visible trials. Second, while the target was occluded, subjects tended to look in the heading direction instead of in the direction of the occluded target. Third, while the target was occluded, participants were more likely to look to the left of the heading direction, i.e., toward the target and not toward a possible future interception point. Because the analyses in previous sections did not reveal differences in eye movements between the different target speed conditions, we use data aggregated at the subject level for the following statistical tests, but note that the results are qualitatively identical when treating the different speed conditions separately.

First, subjects carried out significantly more saccades during occluded trials compared to visible trials. Although the mean saccade frequency in the second trial segment of occluded trials was 0.86 ($SD = 0.26$) saccades per second across participants and target speeds, it was 0.38 ($SD = 0.26$) in visible trials. A paired t test showed that saccade frequency was significantly higher in occluded than in visible trials, $t(17) = 7.89$, $p < 0.01$, $d = 1.86$. This is not easily explainable with the interception location prediction strategy, which would predict only a few saccades to the future interception location and stable gaze at that location thereafter. The off-line tracking hypothesis may predict tracking of the occluded target with smooth pursuit or a sequence of smaller size saccades. Thus, although this result contradicts the trajectory prediction strategy, it cannot rule out the off-line tracking strategy.

Second, while the target was occluded, subjects tended to look in the heading direction instead of in the direction of the occluded target. The proportion of gaze falling within 5° to the left or right of the target during the occluded segment was only 29% ($SD = 11.8$), which was significantly smaller than the aforementioned 88% in visible trials, $t(17) = -34.85$, $p < 0.001$, $d = 8.21$. Instead, a larger proportion of gaze fell within 5° to the left and right of the heading direction in occluded trials (39%, $SD = 12.31$) compared to the visible trials (15%, $SD = 10.72$). A paired t test showed that this difference was statistically significant, $t(17) = 7.01$, $p < 0.001$, $d = 1.65$. According to the interception location prediction

strategy, this is difficult to explain as the possible interception location was not in the direction of current heading of the car but to the right of the heading direction most of the time during interception. Similarly, the off-line tracking hypothesis would predict gaze falling in the believed direction of the occluded target, which, during the visible trials, did not coincide with the heading direction. Although it is not fully possible to exclude that subjects misjudged the putative location of the occluded target to be in the direction of the car's heading, it is highly unlikely, particularly given the experience gained during visible trials.

Third, while the target was occluded, a significantly larger proportion of gaze was directed to the left of the heading direction, i.e., toward the side of the occluded target instead of the direction of possible interception. The proportion of gaze to the left of the heading direction was 94% ($SD = 3.74\%$) in the second segment of visible trials, which is significantly different from 50%, $t(17) = 50.45$, $p < 0.001$, $d = 11.89$. In occluded trials it was 68% ($SD = 19.69\%$), which is also significantly different from 50%, $t(17) = 3.96$, $p = 0.001$, $d = 0.93$. This result is difficult to reconcile with the trajectory prediction strategy as the possible interception location was to the right of the heading direction in both visible and occluded trials. According to the off-line tracking hypothesis, subjects could have tried to maintain gaze on the believed position of the occluded target, which was to the left of the heading direction both in visible and occluded trials. Similarly, the target position was to the left of the heading direction during visible trials, but subjects directed their gaze to the right of the heading direction 32% ($SD = 19.69\%$) of the time during occluded trials. Thus, these results cannot fully rule out that subjects might have tracked the erroneously believed position of the target during occluded trials, but this is unlikely.

General discussion

The CTH strategy

Intercepting a moving target is a fundamental visuomotor task that requires coordinating picking up visual information about the movement of our target with how to steer our own movements. How do humans accomplish this interception behavior? Ample previous research has not converged on a consistent description of how humans accomplish this task in part because some experimental paradigms constrained possible movements. Specifically, studies utilizing speed control tasks prevent subjects from adopting the pursuit strategy and cannot distinguish between the CTH and CB strategy on the basis of measured angular

quantities. In this study, we examined how visuomotor interception is visually guided by asking participants to intercept a moving target with a car using a steering control task in a virtual environment. After appearance of the target, participants adjusted the direction of their movements not by steering toward the current position of the target but instead by steering ahead of the current position of the target along its future trajectory, resulting in curved interception paths. In doing so, the target-heading angle stayed approximately constant, which can be described best with the CTH strategy rather than the pursuit strategy. The target-heading angle changed predominantly early and at the very end of the interception in accordance with previous literature (e.g., Chardenon et al., 2002). By contrast, the target's bearing angle continuously changed at a rate of change significantly greater than that of the target-heading angle. Taken together, this suggests that interceptive steering is better described by the CTH strategy rather than the pursuit strategy or the CB strategy, at least for the specific task conditions and the setup used in our experiment.

The current study furthermore empirically investigated participants' active gaze behavior and visuomotor coordination during interception. In the beginning of a trial, when the target had not yet appeared in the scene, participants looked mostly in the heading direction, similar to previous studies (e.g., Wilkie et al., 2010). During interception, subjects tracked visible targets with smooth pursuit eye movements most of the time as reflected by the small gaze–target angle. This is consistent with previous studies on locomotor interception (e.g., Oudejans et al., 1999; Postma et al., 2014). Similarly, in accordance with previous studies (e.g., Land & Lee, 1994), gaze behavior and steering behavior were coordinated. In the present study, the direction in which participants steered relative to the target direction was highly correlated with the direction in which they directed gaze relative to the heading direction. Thus, the visuomotor control could be described as participants steering so as to maintain the current heading direction relative to the current direction to the target, which corresponds to the visual angle of the target relative to the heading direction. This is different from some previous studies, in which gaze behavior had been related to the bearing angle (e.g., Bastin et al., 2008) or to a trigonometric function of gaze angles relative to the heading angle (e.g., Land & Lee, 1994). As in previous studies (e.g., Guitton, 1992; Land & Lee, 1994), gaze and head directions were coordinated as demonstrated by the high correlation between gaze- and facing-heading angles. The current experiments could not find evidence for the trajectory prediction strategy based on the pattern of gaze shifts and the direction in which subjects looked during interception

of occluded trials. Although the current data can not fully exclude that subjects might have tracked the occluded target during occluded trials, this is highly unlikely given that gaze was directed predominantly in the heading direction or to the right of the heading direction during occlusion of the target, similar to steering without targets.

The current interception maneuvers are seemingly contradicting some previous studies utilizing steering control tasks. For example, Fajen and Warren (2004) reported that the target-heading angle continuously increased in a condition in which the target appeared at a distance of 3 m and an angle of 60° relative to the participant's initial heading, and the target moved toward the participant. By contrast, in a second condition in which the target appeared at the same position but retreated from the participant at an angle of 60°, the target-heading angle stayed approximately constant during interception. Because the mean walking speeds reaching from 1.07 ms⁻¹ to 1.29 ms⁻¹ were comparable across the two conditions, the condition with approaching targets led to relatively shorter interception durations compared to the condition with receding targets. Therefore, due to the inertia in human locomotion (e.g., see Fajen & Warren, 2003, 2007), the interception durations in the former condition might be too short for participants to bring the target-heading angle to a constant value. By contrast, we designed the current experiment so that interceptions usually lasted for about 6–12 s. Additionally, a further difference between these studies is that Fajen and Warren (2004) used the task of interception by walking, and the current study used interception by steering, which involves different end effectors.

Recently, Rushton and Allison (2013) proposed an additional strategy, the “overcompensation” strategy for locomotor interception. According to this strategy, the agent steers so that the change in the heading direction is n times the change in the target-heading,² that is, $\dot{\phi} = n\dot{\beta}$. By varying the value of n , this strategy can produce interception paths with different degrees of curvature, which appears consistent with participants' interception paths in the current study. Nevertheless, the value of n is a free parameter and, therefore, not sufficiently constrained in this model with respect to participants' steering behavior in the current study. Specifically, some particular values of n could lead to a target-heading that continuously changes during interception, inconsistent with the current study. Overall, although the average target-heading angle's rate of change was small but significantly different from zero with a value of 3.07°/s ($SD = 1.07$), the CTH strategy best described participants' steering behavior in this study.

Although the CTH strategy best described the trajectories of our participants' maneuvers, it is a

different question how subjects actually achieved this. The traditional approach to answering this question is to investigate how subjects could potentially obtain necessary information about the geometric quantities involved in the description of the respective strategy. In the case of the CTH strategy, this is the angle between the direction to the target and the heading direction. For participants to be able to use the CTH strategy, the heading direction could be estimated from various sources of information. For example, the heading direction could be determined from optic flow available from the textured ground (Bruggeman, Zosh, & Warren, 2007; Li & Cheng, 2011, 2013; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). As an actor's egocentric axis is usually aligned with the current heading direction (except in "crabbing" gait), the heading direction could be determined from the egocentric axis (Harris & Bonas, 2002; Rushton et al., 1998). This is relevant in car steering in the current experiment because the front of the car was always pointing in the current heading direction (see Wilkie & Wann, 2002). During car steering, the target-heading could be visually estimated as the target direction with reference to the car's egocentric axis, i.e., its antero-posterior axis. It has been shown that heading direction can be determined from podokinetic information alone during locomotion on foot (Telford, Howard, & Ohmi, 1995). During car steering, however, the proprioceptive information from maneuvers of the steering wheel alone is not sufficient to accurately update an actor's heading in an environment (Wallis, Chatziastros, & Bühlhoff, 2002; Wallis, Chatziastros, Tresilian, & Tomasevic, 2007).

Investigating how subjects could potentially obtain necessary information about the geometric quantities involved in the description of the above strategies may nevertheless not be a satisfactory explanation of the observed interception behavior. The reason is that observing a participant intercept a moving target while maintaining angular quantities at a constant value does not necessarily imply that those angular quantities are actively controlled by the subject. A recent study by Belousov, Neumann, Rothkopf, and Peters (2016) proposed a computational model for locomotor interception of fly balls based on optimal stochastic control theory. Crucially, the model considers the agent's sensory uncertainty, internal movement prediction uncertainty, and locomotor control variability as well as sensory delays. Although the model does not represent or calculate angular quantities explicitly, the optimal strategy under certain task conditions results in trajectories along which angular quantities may stay constant. Thus, an outside observer would summarize the strategy as keeping angular quantities constant. Currently, it is still an open question how well this

model can account for interceptive steering in different tasks including the one considered in the current study.

Limitations of current study

In everyday driving, drivers control both a car's heading and speed. In our pilot study, we found that it is very easy for participants to experience motion sickness if they control both the car's heading and speed in virtual environments. It has been shown that motion sickness arises due to a conflict between visual and vestibular information (e.g., see Bos, Bles, & Groen, 2008). Although it is interesting to investigate actors' interceptive behavior as they control both a car's heading and speed, we were not able to do so with the current experimental setup due to the motion sickness affecting participants. However, other experimental setups avoiding motion sickness in interception tasks could be employed. For example, Bastin, Fajen, and Montagne (2010) examined the influence of a car's maximum speed on locomotor interception. In their study, participants controlled both the car's heading and speed to intercept a moving target with the car's maximum speed being varied between participants. They did not report any motion sickness in participants, which may be related to the differences in the experimental setup. We presented the immersive virtual environment in an HMD, and they presented their environment on a large screen (1.8×1.2 m); we provided more natural driving experience with the car being visible, and they did not present any visible features of the car in their display; interception lasted for about 6–12 s in the current study, and it had a shorter duration in their study, for example, about 2.5 and 4.3 s in their example trials. Thus, their experimental setup might help avoid motion sickness. But they did not report any results about the angular variables of concern in the current study. Instead, they showed that a car's maximum speed influences drivers' interception. However, in daily driving, a car's maximum speed does not change. Moreover, when actors could control both their heading and speed during interception on foot, Fajen and Warren (2004) showed that they did not change their walking speed much. For example, in one of their experiments, participants' mean walking speed ranged from 1.1 m/s to 1.3 m/s during the interception. In future studies, we plan investigating appropriate setups to test how actors control both a car's heading and speed to intercept a moving target.

Although the findings in the current experiment are clearly consistent with the CTH strategy, this strategy does not provide a parsimonious explanation of interceptive steering. The reason is that the CTH strategy prescribes the rate of change of the target-heading angle but not its value. By contrast, e.g., the CB strategy is able to account for both the rate of

change of the bearing angle and its value. In previous experiments, e.g., Fajen and Warren (2003, 2007), when actors intercepted a moving target starting with a target-heading angle of 0° , they steered on a curved path and moved in a direction ahead of the target, thereby achieving a positive target-heading angle. Thus, for the CTH strategy to explain the actor's steering, it needs an additional constraint, i.e., keeping the target-heading angle at a value greater than zero. Future research needs to investigate which target-heading angles are preferred in locomotor interception and how the angle depends on factors, such as interception duration or initial target-heading angle.

Conclusion

As participants steered a car to intercept a moving target, they pointed the car ahead of the current position of the target along its future trajectory and the target-heading angle was approximately constant after a brief initial adjustment phase with a value greater than zero. By contrast, the target's bearing angle changed continuously throughout interception. This suggests that interceptive steering is better described by the CTH strategy rather than the pursuit strategy or the CB strategy. Participants' gaze centered with smooth pursuit on the visible target during interception accompanied by small but consistent head angle away from the heading direction toward the direction of the target, suggesting a crucial role of current information in locomotor interception. Target occlusion led to participants' ineffective steering and ultimately to a significantly impaired interception rate. We did not find evidence from participants' eye movements for interception control based on target trajectory prediction.

Keywords: locomotor interception, action control, eye movements, vehicle steering, visuomotor behavior

Acknowledgments

We acknowledge support by the German Research Foundation and the Open Access Publishing Fund of Technische Universität Darmstadt.

Commercial relationships: none.

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Footnotes

¹ This was addressed in detail in Zhao, Straub, and Rothkopf (2017), who examined interception strategies by manipulating the visual information about an allocentric reference.

² It was called target drift in Rushton and Allison (2013), i.e., the change in the target direction with reference to the agent's egocentric reference. It is equivalent to the change in target-heading in the current study.

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